

ON THE RELATIVE ADVANTAGES OF CROSS- AND SELF-FERTILIZATION¹

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ABSTRACT

An optimality model based on the tradeoffs between seed set efficiency and outbreeding is presented that predicts under what conditions selfing should be favored over outcrossing. The model predicts that local density and distributional pattern, degree of environmental predictability, and adult and seed longevity are the independent variables that determine the shape of the marginal benefit curves for seed set and offspring heterogeneity. Some data supporting the model are presented derived from a study of species of the genus *Leavenworthia* (Cruciferae).

Flowering plants can reproduce in two basic ways. All species have the capacity to produce new individuals by vegetative means, such as runners, stolons, bulbs, corms, etc. Nearly all species in addition reproduce by seeds. The embryo contained in the seed is normally the result of the union of the egg cell with a gamete produced by a pollen grain from another plant and transported to the style by some pollinating agent. However, in a number of species, pollen from the same plant occasionally, or habitually, fertilizes the egg. Finally, seeds can also be produced apomictically without recourse to fertilization. From an evolutionary standpoint, the latter is better viewed not as a form of reproduction, but as a means of enlarging the parental genotype. The term vegetative propagation is therefore preferable, reserving the term reproduction for the formation of seed.

The diversity of modes of reproduction encountered in flowering plants presents a challenging problem to the evolutionist. In the present paper I review the most accepted theory and indicate what I consider to be inconsistencies with the requirements of individual Darwinian selection. I then present an alternative model and some arguments in its support. Finally I apply the model to explain the different breeding systems encountered in the mustard genus *Leavenworthia*.

Reproduction produces a number of effects. It results in the production of new individuals possessing a fraction of the parental genes. The same effect results from vegetative propagation. However, reproduction by seeds also very effectively disperses the progeny in space and/or time because seeds have the potential of being transported for long distances and going dormant for variable lengths of time to avoid unfavorable periods in the environment. The selective advantages of dispersal and dormancy have been discussed elsewhere (Crocker,

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1938; Harper, 1957; Harper et al., 1970; Gadgil, 1970; Lewis, 1973). They are a crucial aspect of the life cycle of flowering plants (Harper & White, 1971; Bradshaw, 1972). They do not explain however, the variety of breeding systems, since seeds could be (and in a few species are) produced without recourse to sexuality.

Finally reproduction results in the formation of new recombinant genotypes, an effect not duplicated by vegetative propagation or asexual production of seeds. Since the overwhelming majority of plants and animals reproduce sexually, the formation of recombinant genotypes must be selectively advantageous. What is not clear is exactly in what ways.

THE CLASSICAL HYPOTHESIS

The most commonly accepted hypothesis for explaining the diversity of breeding systems in plants was introduced by Darlington (1939, 1958, ed. 2), and further elaborated by Darlington & Mather (1949), Grant (1958, 1963), Huxley (1942), Mather (1943), and Stebbins (1950, 1957, 1958). Its seminal arguments follow closely the arguments of Muller (1932) for the evolution of sex. According to these authors there is a conflict between producing offspring that possess the superior genotypes of its parents, and species (or population) survival over time. To use the terminology of Mather (1943), there is a supposed conflict between "immediate fitness" (by which is meant individual Darwinian fitness) and "long range flexibility" (the ability to survive over a large number of generations). This conflict is supposed to arise because, according to these authors, "immediate fitness" is best attained by perpetuating the parental genotypes, which are envisioned to be superior since they have survived to reproductive age, while "long range flexibility" requires mechanisms that allow for genetic change over time. To quote Darlington (1958: 234), "Sexual reproduction survives because it profits all posterity. The opposite state of apomixis survives because it profits its own immediate progeny." Or in the words of Stebbins (1950: 170), "Sex exists . . . for any [no] other reason than its function in securing a great variety of genetic recombinations, by which the evolutionary line may adapt itself to new and varied environments."

This hypothesis makes the fundamental assumption that the fitness of a phenotype is dependent mostly on its genic endowment, that the parental genotype is always more fit in its immediate environment, and that the selective forces of the environment vary only slowly over space and time. Furthermore, the mechanism that it adduces for the selection of sexuality is intergroup or interdeme selection, since it is easy to show that within each population, selection should favor (if the assumptions of the hypothesis are correct) apomicts and/or selfers (Karlin & McGregor, 1974). Cogent arguments against group selection in the evolution of sex have been presented by Maynard Smith (1971) and Williams (1975). Arguments in favor of viewing the selected forces as oscillating in space and time are discussed in Solbrig & Simpson (1974) and Levin (1975) and will be elaborated further on.

AN ALTERNATIVE HYPOTHESIS

I now present an alternative cost-benefit hypothesis based on two assumptions: (1) there is an oscillating environment, and (2) all selection is individual Darwinian selection. The hypothesis balances the costs of outcrossing over self-fertilization against possible benefits from outcrossing and leads to prediction about when a plant should self and when it should increase its inclusive fitness by crossing.

We must remember that the breeding system that will be favored and ultimately selected is the one that maximizes the inclusive fitness of the parent (Hamilton, 1964). That means, the breeding system that leads to an increase of the parental genes in the following generation.

THE COSTS OF OUTCROSSING

There are two major costs associated with outcrossing. One is intrinsic to the sexual process, the second is peculiarly botanical. When an offspring is produced by self-fertilization or apomixis, it receives all its genes from one parent; when an offspring is produced by crossing, half of the offspring's genes come from one parent, the other half from the other. Some of the alleles received from the two parents are identical by descent, so that the offspring may have more than a 50% genetic similarity with each parent. Similarity rises as the number of alleles shared by the parents increases, reaching a theoretical maximum of 100% in genetically identical parents. Since fitness is the proportional contribution of genes to the next generation, each offspring produced through the sexual process contributes less to the parental fitness than offspring produced by asexual means or by selfing. Maynard Smith (1970), Williams (1975), and Williams & Mitton (1973) have termed this the "meiotic cost."

For cross-fertilization to occur in flowering plants an outside agent must carry the pollen from one plant to another. Angiosperms rely on either physical agents (wind, water) or animals (insects, birds, bats) to carry the pollen from one plant to another. This transport of pollen carries with it an energetic cost because of the mortality of pollen grains that never reach a receptive stigma (particularly high when the agent is wind or water) and because of the cost of producing structures to attract and reward animal agents (showy petals, nectar). This energetic cost results in less energy available for seed production and/or other activities compared to plants which reproduce apomictically or by selfing.

In addition, self-fertilization and especially apomixis is inherently more efficient as a method for producing embryos. Crossing requires two flowers in different plants blooming at the same time and an outside agent transporting the pollen during that period. Even under the best of circumstances some ovules remain unfertilized, and under unusual conditions (rain, cold) the failure to set seed can be significant, as is well known from silviculture and pomology.

THE BENEFITS OF OUTCROSSING

While there is general agreement regarding the cost of outcrossing, there is no consensus regarding the benefits derived from producing a genetically vari-

able progeny. There are, however, very clear benefits that can be obtained by a plant that produces variable offspring, provided the plant lives in a spatially and temporally varying environment.

The environment is treated as a constant in most discussions of breeding systems (Darlington, 1939; Stebbins, 1950; Grant, 1958), probably because most investigators have considered the physical environment. Some components of the physical environment (e.g., day length) are very predictable, but others (e.g., rainfall) are not, creating conditions under which variable progeny may be advantageous. However, interactions with other plants, herbivores, pathogens, and pollinating and seed dispersal agents also strongly influence reproductive success. This "biological environment" is very complex and is constantly changing, often at rapid rates relative to generation times of populations of plants. Furthermore, while the features of the physical environment are only marginally affected by the biological milieu (e.g., runoff patterns and precipitation can be affected by vegetation), the biological environment responds to the activities of the plant. For example, given a certain water and light regime, there is one or a fixed few optimal leaf forms that maximize photosynthesis. Once those leaf forms have been attained there will be no further response to the physical environment, nor is there a response from the environment. Similarly, a leaf predator exerts selection for the evolution of defenses against it, but as soon as those defenses begin to evolve, they become selective agents on the herbivore, favoring herbivore phenotypes that can break the plant's defenses. Also, most pathogens and herbivores have shorter generation times and larger population numbers than their hosts and can readily respond genetically to any defense the plant puts up.

In this context the immediate advantage of producing variable offspring is clear. While a plant with a leaf shape optimal for the physical environment (light and heat) may maximize its fitness by transmitting that shape to its progeny, the plant that produces offspring having exactly the same defense against a predator or pathogen risks losing all its offspring if and when the predator or pathogen breaks that defense. Therefore it will have a higher probability of producing viable offspring if each has a different kind or degree of defense against the predator and pathogen. The same argument applies for competitors. In the metaphor of Williams (1975), the chances of winning a lottery are not increased by xeroxing the same number, but by having a great variety of different numbers. See Levin (1975) for further discussion of this point.

The problem is further accentuated by the fact that plant seeds have a very limited choice of where they will grow. Consequently, the density, cover, and distance to competitors that each individual offspring seedling encounters are different from those of the parent plant and also from each other. Furthermore, they cannot avoid pathogens or predators by escape. Under these circumstances, production of only one phenotype drastically reduces the chances of success of many of the seedlings and, consequently, reflects on the fitness of the parent.

THE COST-INCOME ANALYSIS

Any model of natural selection acting on a trait assumes that fitness or some component of fitness is being maximized or optimized relative to others. It also

assumes that the organism is operating within some externally (or internally) applied constraints. Fitness is clearly increased both by enlarging the seed crop and by the previous argument as a result of increased genetic heterogeneity of the offspring. The constraint is the available energy for reproduction, so that the seed crop and devices to increase the dispersal of pollen cannot be enlarged indefinitely. The problem is to find what proportional allocation of resources to these competing processes maximizes fitness.

While the costs of seed production and pollinator attraction can be measured in calories, the benefits of increased seed crops or polymorphic progeny cannot, and have to be measured in terms of relative fitness. To keep these two measures clearly separate I use the following terminology: cost = energetic input by the plant, in calories; benefit = increase in fitness; investment = cost associated in increasing fitness; marginal benefit = increase in benefit/unit of investment.

Because of insufficient information on the benefits derived from seed production and a genetically heterogeneous offspring, the arguments are based on general shapes of curves, the conclusions being based not on their exact shapes, but on their relative position to each other.

BENEFITS AND COSTS ASSOCIATED WITH OUTCROSSING

The benefit is proportional to the degree to which the progeny is unrelated to each other, that is, it will be inversely related to the coefficient of inbreeding. Assuming random breeding, the coefficient of inbreeding, F , is given by (Falconer, 1960):

$$F = 1/2 N_e$$

where N_e = the effective size of the breeding population.

The number of potential mates is correlated with the area reached by pollen (the pollen shadow) and the density of potential mates in that area. Assuming that the pollen shadow is approximately circular:

$$N_e = \pi r^2 k = \alpha r^2$$

where r = radius of the pollen shadow, and k = the density of potential mates per unit surface.

The probability of mating is, however, not random as assumed, but decreases with distance as a result of the well known leptokurtic distribution of pollen (Bateman, 1951), so that:

$$PD_x = PD_o e^{-x/a}$$

where PD_o = total pollen produced by the plant; PD_x = pollen density at distance x , and a = a factor that affects the shape of the pollen density distribution and depends on the kind of pollinator.

The potential benefit is then a function of plant density, the maximum diameter of the pollen shadow, and the shape of the pollen distribution curve, which depends on the total amount of pollen produced and the movements and effectiveness of pollinators.

The costs are also defined by the above equation and are the costs of pollen production (PD_o), and the costs associated in increasing the value of a , the pollinator attraction devices. When the pollen vector is a physical factor, the costs of pollinator attraction are minimal, being restricted to morphological changes in the style and the anthers. Wind or water as a pollinating agent produces very leptokurtic pollen distributions and results in high pollen mortality rates (Whitehead, 1969; Gleaves, 1973).

Additional costs associated with animal pollinator attraction are the production of showy flowers and rewards: scents, pollen, nectar, oil (Faegri & van der Pijl, 1971). Pollinators that carry pollen over large distances, such as large bees, birds, or bats, visit only flowers that offer large rewards. The amount of necessary reward is apparently positively correlated with the distance that the pollinator covers between plant mates (Opler, personal communication) although good published data are unavailable. In any case, increased gamete wastage is associated with pollination distance regardless of the pollen vector. The apparent greater efficiency of animal pollinators in relation to physical agents is compensated by the greater costs of attraction (Fig. 1). In either case, the costs of pollen production and pollinator attraction increase with the diameter of the pollen shadow, and result in fewer flowers produced and an increased pollen/ovule ratio for a given energetic commitment to reproduction.

Maximization of inclusive fitness in the present context translates into producing a pollen shadow ample enough to insure adequate genetic heterogeneity in the progeny, but not so large as to over-depress seed production by the mother plant. That is, the breeding system that maximizes fitness is the one where the reproductive energy has been invested so as to yield the greatest marginal benefit. The exact compromise between seed number and progeny heterogeneity depends on the plant's reproductive effort, the distribution and density of mates, and the life history of the plant.

Figure 2 depicts graphically how changes in patchiness and density affect the benefit derived from investments in structures that increase progeny heterogeneity. The benefit obtained for a given investment is affected by the density and the distributional pattern. This is intuitively obvious if one thinks of a plant that is wind pollinated: the lower the density of mates, and the more clumped, the greater the number of pollen grains that land in places other than receptive stigmas. Although less obvious, it is equally valid for animal pollinated plants. An efficient user of plant floral rewards should spend more time within a clump than flying from clump to clump. Furthermore, isolated plants will be under-visited. Another very important effect of a clumped distribution is that the inbreeding coefficient within a clump increases rapidly as a result of gene fixation in small populations, the so-called Wahlund effect (Wallace, 1968). This will create a threshold effect: little benefit is obtained from outbreeding until the pollen shadow is sufficiently large to cover more than one clump.

BENEFITS AND COSTS ASSOCIATED WITH SEED PRODUCTION

Figure 3 depicts the benefit derived from increased investment in seed production. I have no way of assessing the exact form of the curve, but I presume that

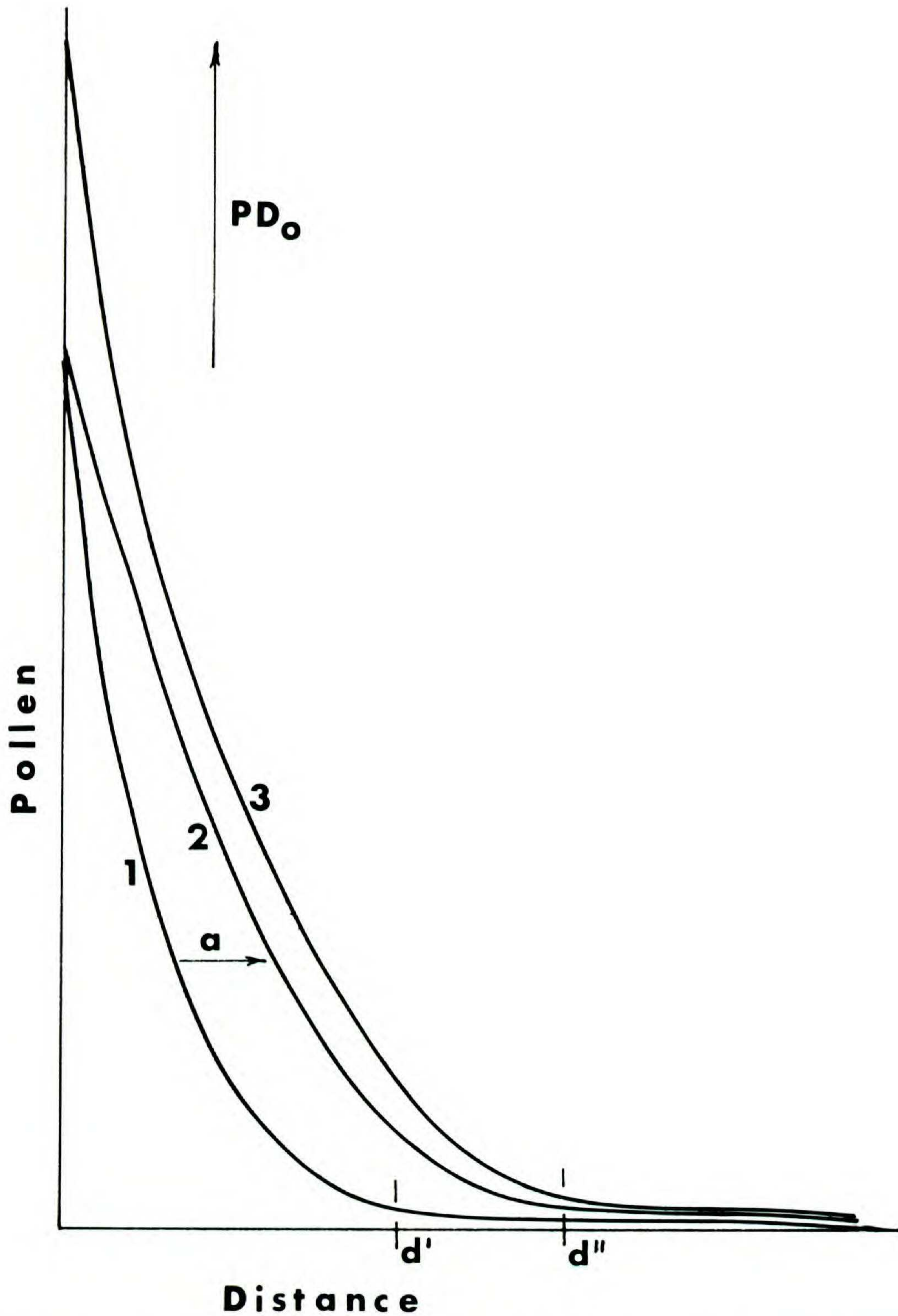


FIGURE 1. Relationship between pollen amount and distance of pollen shadow in one dimension. Curve 1 represents a random leptokurtic distribution. The effective distance of the pollen shadow is d' , although some pollen will travel larger distances. To increase the effective distance to d'' , either the shape of the curve has to be changed by switching to a more effective but expensive pollinator (curve 2) or total pollen production has to be increased (curve 3).

it is either linear or more likely negatively exponential, since as the number of seed increases, the relative contribution that each makes to the total genetic heterogeneity decreases (assuming gene frequency remains constant). It is reasonable to suppose also that the value of each seed is in general lower for plants

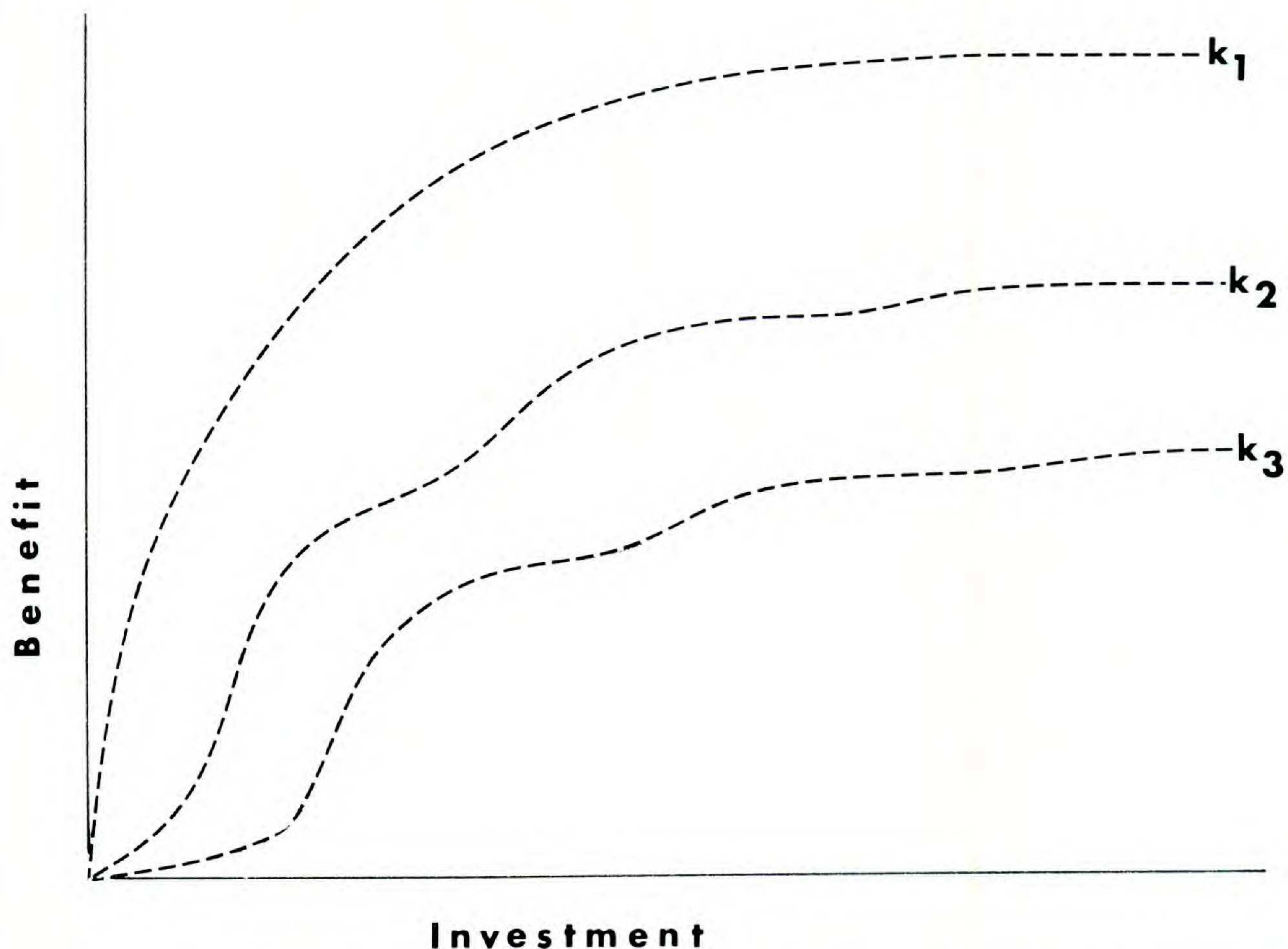


FIGURE 2. Relationship between benefit and investment in structures that increase offspring genetic heterogeneity for three levels of density and patchiness. Density of $k_1 > k_2 > k_3$; patchiness in $k_1 < k_2 < k_3$.

with long generation times, or in more rigorous terms, the value of a seed is directly correlated with its probability of germinating and growing, and is therefore correlated with the factors that control the life strategy of the species (Schaffer & Gadgil, 1975).

The costs associated with seed production are of three main kinds. First are the costs of producing the embryo and the seed coats. Seeds are usually rich in proteins and fats and have a high caloric content per gram of seed. Second are costs associated with seed dispersal (fleshy fruits, wings, spines, hairs), and finally there are the costs associated with defending seeds against predators. Caloric content is easily measured, but costs of dispersal and defense are quantified only with difficulty, and then only approximately (Harper et al., 1970; Janzen, 1969). Seed costs consequently vary from species to species, and trade-offs between investment in seed size, defense, dispersal, and seed number are to be expected (Harper et al., 1970).

THE OPTIMAL STRATEGY AND GENERAL PREDICTIONS

Figures 4A and 4B shows the marginal benefit (dB/dI) derived from different levels of investment in offspring heterogeneity and seed number for two opposite evolutionary strategies.

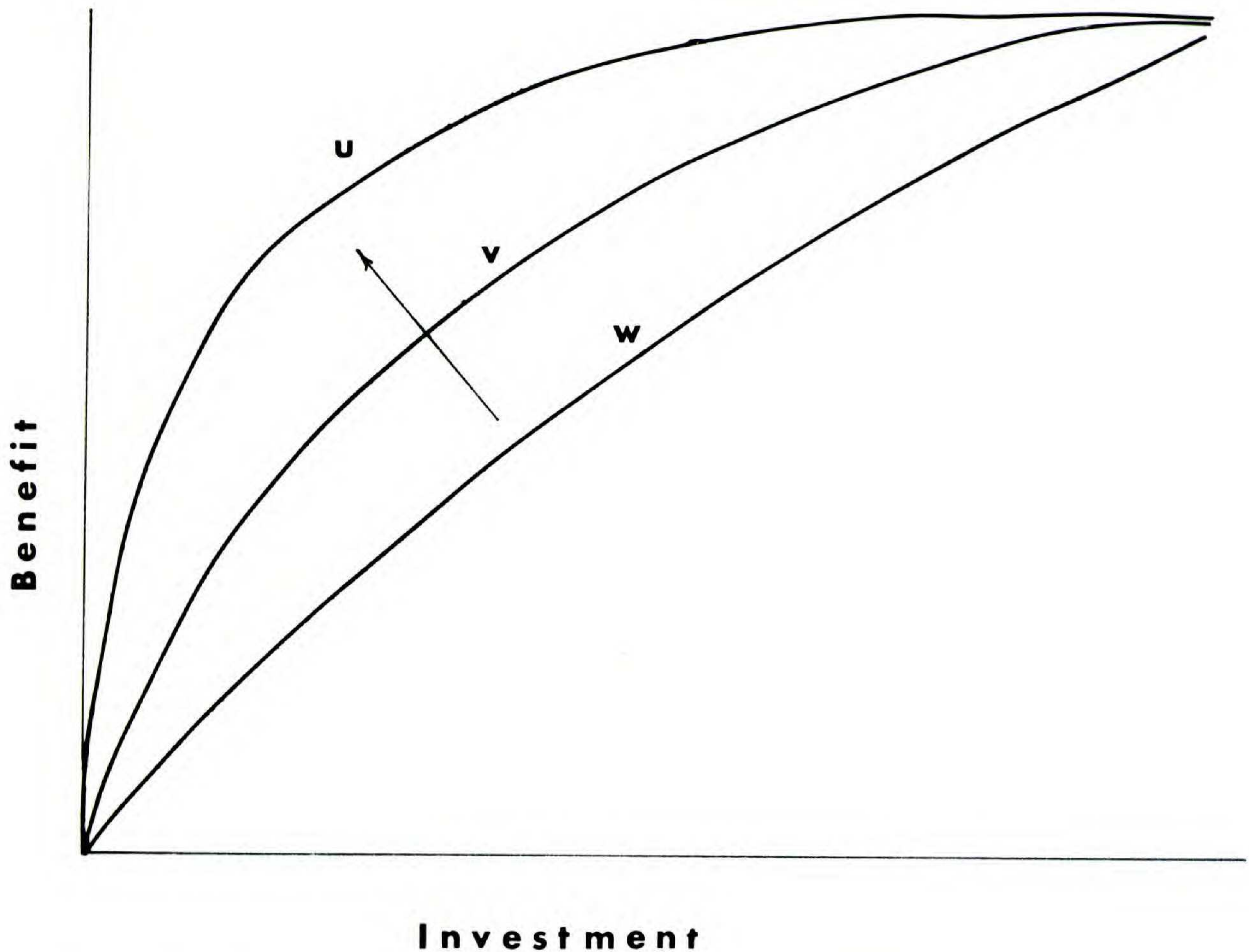


FIGURE 3. Relationship between benefit and investment in seed number for three species with different life history strategies; "r" selection increases from w to u.

Figure 4A analyzes the so-called "K" strategy (Gadgil & Solbrig, 1972). An example would be a long-lived forest tree exposed during its life-time to a variety of states of the physical environment, and subject to attack by a diversity of parasites and herbivores, as well as potential competition from many different species of plants. I further assume that such a species is more or less evenly distributed in the forest. Furthermore, because of adult longevity, replacement events should be relatively rare. A concrete example is the common beech, *Fagus grandifolia*. Under these conditions I predict that the marginal seed benefit curve will be relatively flat until a maximum is reached at relatively high investment levels (curve W, Fig. 4A). The marginal benefit curve from outcrossing should start high, reaching a maximum at relatively low levels of investment and then dropping quickly (curve K_2 , Fig. 2). Although reproductive effort will tend to be low, since the plants are large and long lived, absolute investment in reproduction tends to be medium to high. Under those conditions, the analysis predicts a reasonable investment in structures to increase genetic heterogeneity through cross-fertilization, and a seed crop that should increase in direct proportion to total reproductive investment.

Figure 4B depicts the extreme opposite, "r" strategy. This is typically a fugitive species, with generations shorter than a year, exploiting a temporary resource. It grows primarily in open situations where interspecific competition is

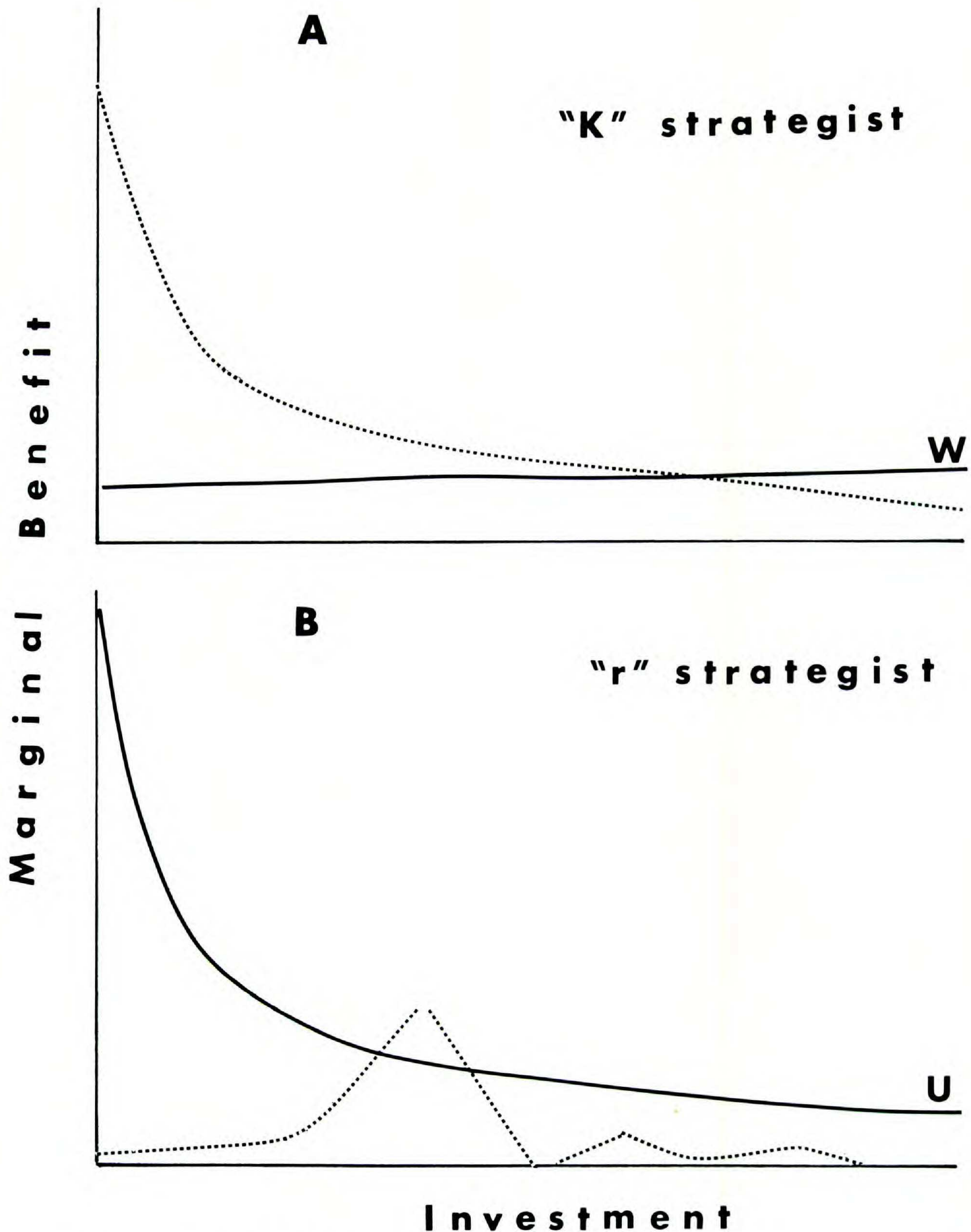


FIGURE 4. Relationship between marginal benefit and investment for an extreme "K" and "r" strategist. The marginal benefit curves obtained from Figs. 2 and 3 (tangent to total benefit) and labelled accordingly. Solid line is the value of the tangent of lines W and U from Fig. 3; dotted line is the value of the tangent line k_2 (upper) and k_3 (lower) from Fig. 2. In the "K" strategist, selfing is favored only for very low levels of investment in reproduction. However, after a certain point it is more profitable to increase the seed crop. For the "r" strategist selfing is favored for low and medium levels of investment. Further details in text.

low, and it can to some extent escape from predators and parasites due to its short life cycle and spatial unpredictability. Density will be locally high but the overall distribution will be very patchy. As a result, genetic drift (Wahlund effect and founder principle) will be important and local populations will tend to inbreed. A concrete example is the common horseweed, *Conyza canadensis*. I predict that because of the frequent replacement events and the high degree of density independent mortality, the initial marginal benefit from investment in seeds is high and decreasing thereafter (curve U, Fig. 4B). On the other hand, because of the genetic uniformity of local populations the marginal benefit of genetic heterogeneity raises slowly with investment (curve K_3 , Fig. 2). Only when the pollen shadow gets large enough to encompass several subpopulations, will the benefit derived from offspring heterogeneity raise sharply. The analysis indicates that selfing is the best strategy for low and medium levels of investment in reproduction. However, for high levels of investment, there is a great marginal benefit in diverting part of the energy to the production of structures that insure outcrossing.

Between these two extremes an infinite number of combinations of seed and genetic heterogeneity marginal profit curves is possible. The exact shapes and combinations will depend on each species. However, the following general predictions can be advanced.

1. Cross-pollination should be the favored breeding system in flowering plants. In effect, selfing as a mechanism is favored only where total reproductive investment is low and where initial marginal benefit from investing in enlarging the pollen shadow is low.

2. Selfing should be more prevalent in species with small populations and clumped distributions. This is a direct consequence of the tendency of small populations to inbreed regardless of the breeding system.

3. Selfing should be more common in plants with short life cycles. This prediction follows from the increase in the marginal benefit of initial investment in seed at the expense of outcrossing and because short-lived plants tend to be smaller and can invest less energy in reproduction (although they devote a larger proportion of their available energy to reproduction).

4. Environments with low predictability will favor outbreeders, while very predictable environments will not favor them as much. This follows from the initial assumption of the model.

These predictions are testable, although a rigorous test of the model has to wait until values for the investment-benefit curves have been obtained.

THE TEST OF THE MODEL

The model can be tested in two principal ways. The first is to obtain general correlations of breeding system with pollen-shadow diameter, distribution pattern, and longevity, as well as with the appropriate measures of density and pattern, and seed number and size, in natural taxa. Stebbins (1950, 1957) and Fryxell (1957) have presented general surveys and the general correlations that they find are in agreement with the model's predictions. Additional data can be found in Baker (1965, 1972), Fukuda (1967), and Levin & Kerster (1974).

TABLE 1. Number of flowers, number of fruits, pollination efficiency, and seeds per fruit in species of *Leavenworthia*.

Population and Species	Year	No. of Plants	No. of Flowers /Plant	No. of Fruits/Plant	Pollination Efficiency	Seeds/Fruit
<i>exigua</i>						
7165*	1975	50	13.0	12.2	0.94	—
7222*	1974	50	7.4	5.7	0.77	3.90
7167*	1974	50	6.6	4.8	0.73	3.70
7168*	1974	50	4.1	3.2	0.78	2.6
7168*	1975	50	5.9	5.2	0.89	—
<i>alabamica</i>						
7216	1974	50	10.9	8.5	0.78	6.10
7202*	1974	50	91.5	69.1	0.76	6.26
7202*	1975	50	39.1	34.6	0.89	—
<i>crassa</i>						
7206	1974	50	5.5	3.3	0.60	3.07
7210	1974	50	12.7	7.9	0.62	1.78
7208*	1975	50	5.1	4.1	0.80	—
<i>stylosa</i>						
7411	1974	50	3.7	2.0	0.54	3.0
7412	1974	50	7.3	4.2	0.56	3.3
7413	1974	50	12.8	6.7	0.52	3.8
7414	1974	50	8.5	5.1	0.60	4.3

Species marked with an asterisk (*) are self-compatible and at least in part self-pollinating.

A second way of testing the model is by searching for these relations in a specific taxon. I now present data from a field study of the genus *Leavenworthia* and compare the results with the predictions made by the model.

THE GENUS *LEAVENWORTHIA*³

This is a small group of winter annuals in the family Cruciferae (Rollins, 1963). The seven species of the genus can be divided into two groups each containing three diploid species, and a third group formed by a single polyploid species. One of the groups is formed by two species, *L. alabamica* and *L. crassa*, which have both self-incompatible and self-compatible populations (Rollins, 1963; Lloyd, 1965), as well as a derived self-compatible and largely self-pollinated species, *L. exigua*. These species have 11 pairs of chromosomes. The other group is formed by one self-incompatible species, *L. stylosa*, and by two self-compatible species, *L. torulosa* and *L. uniflora*. Of these, *L. uniflora* is largely self-fertilizing, but *L. torulosa* appears to be mostly outbred. These species have 15 pairs of chromosomes. All species grow on calcareous outcrops primarily in Tennessee and northern Alabama, known locally as glades.

The existence of these very closely related species with different breeding systems, and of two species with some populations that are selfers and some that are not, presents an unusual opportunity to test the model. If the model is cor-

³ The study on *Leavenworthia* made in collaboration with R. C. Rollins.

TABLE 2. Abundance, density, frequency, and approximate size of populations in species of *Leavenworthia*.

Species and Population	Year	N	Abundance	Density	Frequency	Deviat. χ^2	Randomn. var/mean	No. of Plants/Pop.
<i>exigua</i>								
7165†	1975	28	88.63	30.67	21	0.26	3.939 ***	5,000
7167†	1974	50	145.89	29.18	20	218.65 **	9.603 ***	9,000
7167†	1975	49	134.09	35.61	27	67.50 *	5.343 ***	11,000
7168†	1975	39	208.33	21.21	10	4.293	15.48 ***	6,000
<i>alabamica</i>								
7501-a	1975	17	128.79	75.75	5	2.686	0.48	19,000
7501-b	1975	68	94.70	11.14	12	3.849	11.23 **	35,000
7501-c	1975	20	92.42	41.67	45	0.488	0.764	160,000
7502	1975	26	151.52	23.48	15	4.251	6.622 ***	58,000
7216	1975	5	75.76	15.15	20	0.668	0.5218	11,000
<i>crassa</i>								
7206	1974	50	196.18	28.05	14	226.79 **	14.25 ***	100,000
7206	1975	100	142.42	11.37	8	10.080**	30.84 ***	45,000
7210a	1975	18	136.36	37.88	28	33.189**	3.166 *	6,000
7210b	1975	43	279.55	123.48	44	188.36 **	4.276 ***	150,000
7208a†	1975	22	75.76	3.79	5	0.657	16.91 ***	850
7208b†	1975	52	75.76	4.55	6	1.044	15.55 ***	2,700
<i>stylosa</i>								
7411	1974	50	204.96	106.23	38	3882.33 **	10.38 ***	310,000
7411	1974	50	490.15	146.97	30	139.46 **	9.086 ***	440,000
(seed- lings)								
7411	1975	100	215.90	43.18	20	6447.36**	10.792 ***	130,000
7503	1975	43	118.94	18.94	16	99.57 **	8.44 ***	38,000

Population marked with a dagger (†) are self-compatible.

* P 0.05

** P 0.01

*** P 0.001

rect, we expect to find tradeoffs in the genetic structure of the populations, the pollination mechanisms, and in seed-set efficiency. They should be correlated with different marginal benefit curves as a result of different environmental parameters controlling the density and pattern of growth. The research design, in-depth description of the biology of these species, and discussion of the results are discussed elsewhere (Solbrig & Rollins, in press). I here present only a brief summary of the results pertinent to this discussion.

Genetic diversity was measured through the use of isoenzymes, as well as through a study of variation of three fruit characters. As predicted, populations of self-compatible and presumed selfers showed less genotypic variation, and a correspondingly high value of F (Solbrig, 1972). The analysis of the morphological variation showed a significantly higher between-family component of the variance in self-compatible populations than expected by the null hypothesis. It also was found that, regardless of the breeding system, small and more clumped populations were more inbred than larger populations. Consequently, it can be concluded that the benefits derived from outcrossing in the small and in the self-

compatible populations rise slower with investment (pollen-shadow diameter) than in the large and in the self-incompatible populations.

Self-incompatible populations are exclusively pollinated by insects, while populations of self-compatible plants are both self-pollinated and cross-pollinated by insects. However, populations of self-compatible plants invest less in pollinator attraction: flowers are smaller (Rollins, 1963; Lloyd, 1965), and they have a lower pollen/ovule ratio (Lloyd, 1965). However, seed-set efficiency, as measured by the ratio of flowers/fruits is greater in the selfers (Table 1). Both these results are expected if the model is correct.

The model further predicts that the changes in breeding system are the consequence of different marginal values of offspring heterogeneity and seed number resulting from changes in density and local distributional patterns of the populations. The density and pattern of several populations was measured (Table 2). It can be seen that there is a clear difference between selfers and outbreeders: the density and the size of the population of self-compatible (and presumed selfing) populations is significantly smaller than that of the self-incompatible populations. In these small populations (that, as was pointed out above, are genetically uniform) outbreeding increases offspring genetic heterogeneity very little. Consequently, the marginal value of producing structures to increase outbreeding is below the marginal value of producing additional seed, and it is more profitable (greater fitness) to decrease the investment in factors that promote outbreeding and transfer them to seed production by the more efficient selfing method. As seed number increases, the marginal value of each additional seed beyond a point (maximum) decreases until it becomes again profitable to invest in factors that promote outbreeding. The exact point depends on each population, and has been carefully documented by Lloyd (1965) for *L. alabamica* and *L. crassa* and by Solbrig & Rollins (in press) for *L. exigua*.

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